

CHYROMYIDAE (DIPTERA) FROM THE GALÁPAGOS ISLANDS, ECUADOR: THREE NEW SPECIES OF *APHANIOSOMA* BECKER

TERRY A. WHEELER¹ AND BRADLEY J. SINCLAIR²

Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.

Abstract.—Three new species of the genus *Aphaniosoma* Becker are described from the Galápagos Islands, Ecuador: *Aphaniosoma arenicolum* Wheeler, n. sp. from the islands of Española, Isabela, Rábida, Santa Cruz and Santa Fé; *Aphaniosoma galamarillum* Wheeler, n. sp. from the islands of Isabela and Santa Cruz; and *Aphaniosoma rabida* Wheeler, n. sp. from the island of Rábida. These species are the first members of the family Chyromyidae described from the Neotropical Region.

Aphaniosoma arenicolum appears to be closely related to a group of southern Nearctic species. *Aphaniosoma galamarillum* is the probable sister species to the Hawaiian species *A. minutum* Hardy. The affinities of *A. rabida* are unknown based on present knowledge of the genus. Ancestors of the three species probably arrived in three separate colonization events via rafting by adults or larvae or as aerial plankton. The source area of these ancestors cannot be determined at present because there is no phylogenetic hypothesis about relationships between the species of the genus and because there has been little collecting on the west coast of Central and South America, the most likely source area.

Male postabdominal structure in the genus *Aphaniosoma* is briefly discussed and some errors and omissions in previously published treatments of chyromyid terminalia are clarified.

Key Words: *Aphaniosoma*, Chyromyidae, Neotropical, Galápagos, systematics, morphology

The family Chyromyidae is a small (approximately 50 described species), primarily Holarctic family of acalyptrate Diptera. Specimens of the family are collected infrequently and little is known of their biology and immature stages (McAlpine 1987). Adults have been collected in bird's nests, mammal runs, decaying wood, on vegetation around pond and creek margins, in

caves, and on windows (Soós 1984, McAlpine 1987). Most species of the genus *Aphaniosoma* Becker are found only in vegetation on seashores and around alkaline or saline ponds (McAlpine 1987).

Aphaniosoma is the largest genus of Chyromyidae, with more than 30 described species in most zoogeographic realms. The only record of the genus in the Neotropical region is a report of a single damaged specimen from the Bahamas identified as *Aphaniosoma* sp. (Melander 1913). During an ongoing survey and analysis of the insect fauna of the Galápagos Islands, coordinated by S. B. Peck (Carleton University), three previously undescribed species of *Aphanio-*

¹ Present Address: Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1.

² Present Address: Entomology Section, Australian Museum, Box A-285, Sydney South, NSW 2000, Australia.

soma were collected in the littoral zone on the islands of Española, Isabela, Rábida, Santa Cruz, and Santa Fé. These three species represent the first Neotropical records for the family Chyromyidae other than Melander's questionable Caribbean record.

MATERIALS AND METHODS

Sources of material and specimen preparation.—The following museums (abbreviations in parentheses) were sources of material examined in this study: California Academy of Sciences, San Francisco, CA, U.S.A. (CAS); Canadian National Collection of Insects, Ottawa, Ontario, Canada (CNC); National Museum of Natural History, Washington, D.C., U.S.A. (USNM).

Specimens were collected into ethanol and subsequently critical-point dried. For genitalic preparations, abdomens were detached from mounted specimens, macerated in warm 85% lactic acid, and immersed directly in glycerin for further dissection and examination. Dissected abdomens were transferred to fresh glycerin for storage in microvials.

Morphological terminology.—Morphological terms used in this paper follow McAlpine (1981) except for some structures of the male and female postabdomen. Recent studies on postabdominal structure throughout the Diptera (Cumming and Sinclair 1990, Wood 1990, 1991) have identified errors in the terms of McAlpine (1981) and have resulted in a revised system of terms that is consistent in its interpretation of homology throughout the Diptera. The following description summarizes the revised system of terms as it applies to the Chyromyidae (equivalent terms of McAlpine in parentheses). The phallus (aedeagus) is comprised of a small basiphallus and a large distiphallus; movement of the phallus is mediated by the phallapodeme (aedeagal apodeme), a structure derived from the hypandrial complex and not homologous to the aedeagal apodeme of the Nematocera and Lower Brachycera. The

phallapodeme is broadly connected to the hypandrium by a ventrally or anteroventrally directed phallic guide (aedeagal guide); the phallic guide is reduced or absent in the species described in this paper. The gonostyli (parameres, postgonites of other authors) are articulated to the posterior margin of the hypandrium and project posteroventrally lateral to the distiphallus. Each gonostylus is not articulated directly to the hypandrium but via an intermediate sclerite, the pregonite (gonopod). The pregonites are often secondarily fused with the hypandrium or absent, as is the case with the species described in this paper. The bacilliform sclerites (sternite 10) arise from sclerotization of the intersegmental membrane between the phallus and the proctiger and articulate anteriorly to the basiphallus and posteroventrally to the surstyli.

Two deviations from McAlpine's (1981) terms occur in descriptions of the female postabdomen. The dorsal and ventral sclerites between the sclerites of segment 8 and the cerci are referred to as tergite 10 and sternite 10, respectively. Although McAlpine (1981) accepted that a true epiproct and hypoproct (i.e. tergite and sternite of segment 11) are absent in the Schizophora, he retained those terms for the dorsal and ventral sclerites posterior to segment 8. Griffiths (1981) pointed out this discrepancy in McAlpine's terminology and cited morphological studies that show the sclerites are those of segment 10.

Genus *Aphaniosoma* Becker

Aphaniosoma Becker, 1903: 186. Type species: *Aphaniosoma approximatum* Becker (monotypy).

Diagnosis.—Chyromyidae with all fronto-orbital bristles reclinate, lost in some species. Occipital region of head concave. Proepisternal bristle usually present. Scutellum with four marginal bristles, without dorsal bristles or setulae.

Biology and distribution.—Most species

of *Aphaniosoma* occur in arid, saline habitats; specimens are most frequently collected on marine shorelines and at the margins of alkaline or saline inland waters (McAlpine 1987).

Most described species of *Aphaniosoma* are Palearctic, with 26 species recorded from the region (Soós 1984, Ebejer 1993). There are three Nearctic species (McAlpine 1987), three Afrotropical species (Cogan 1980), one Oriental species (Steyskal 1977), and two species in the Australasian/Oceanian Region (Pitkin 1989). Records of *Aphaniosoma* from regions other than the Nearctic and Palearctic are only from islands, not from the continental landmass. The Afrotropical records are from the Cape Verde and Canary Islands, St. Helena, and the Seychelles (Cogan 1980), the single Oriental species is known from Taiwan (Steyskal 1977), and the Pacific species are known only from Hawaii (Pitkin 1989).

Remarks.—As the generic diagnosis suggests, species of *Aphaniosoma* are recognized only on the basis of external characters. There has been no comparative study of the postabdomen in the Chyromyidae and, consequently, there are no established postabdominal synapomorphies for the genera. Variability in external characters both within and between chyromyid genera and variability within genera in the male postabdomen suggests that the presently recognized genera, including *Aphaniosoma*, may not be monophyletic. Nevertheless, we retain *Aphaniosoma* as presently defined on external characters, pending a comprehensive phylogenetic treatment of the family.

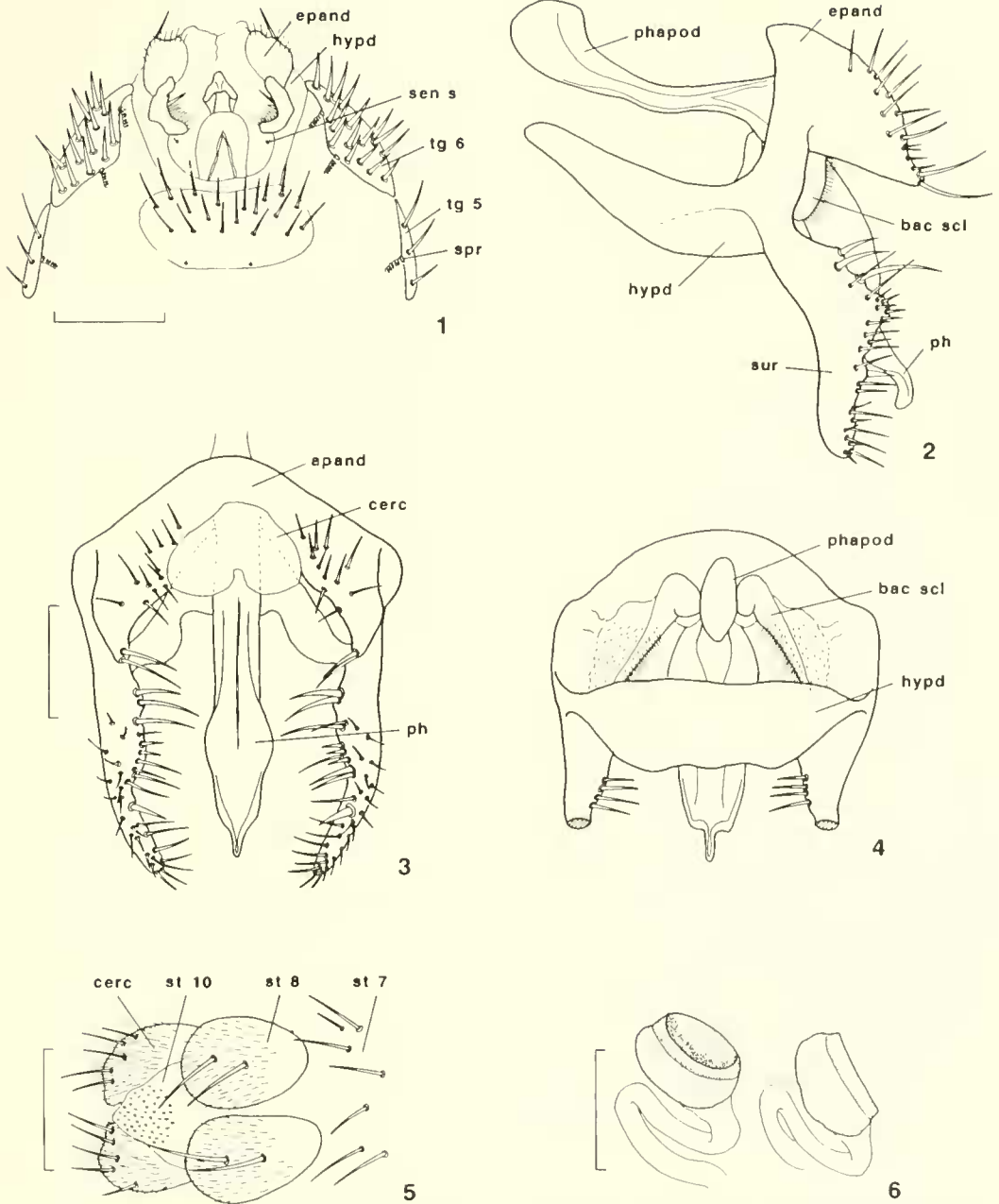
KEY TO ADULTS OF THE GALÁPAGOS SPECIES OF *APHANIOSOMA*

- 1. Head mostly yellow, occiput and ocellar tubercle gray; fronto-orbital bristles absent, row of short fronto-orbital setulae present, slightly longer posteriorly; interfrontal setulae slightly reclinate. Scutum gray anteriorly, yellow on lateral and posterior margins. Abdominal tergites dark gray with yellow margins *A. arenicolum* n. sp.

- Head entirely yellow; 2 or 3 pairs of fronto-orbital bristles present; interfrontal setulae proclinate. Scutum and abdomen yellow 2
- 2. Total length 1.1–1.4 mm (critical-point dried specimens). Three pairs of reclinate fronto-orbital bristles present. Male hind basitarsus broad and flat, approximately twice as wide as second tarsomere and as long as rest of tarsomeres combined. Male surstylus with pectinate ventromedial bristle (Fig. 8), male bacilliform sclerite bare (Fig. 8). Female sternite 10 uniformly spinulose (Fig. 9) *A. galamarillum* n. sp.
- Total length 1.4–1.9 mm (critical-point dried specimens). Two pairs of reclinate fronto-orbital bristles present. Male hind basitarsus not flattened, only slightly wider than second tarsomere, not as long as rest of tarsomeres combined. Male surstylus with short, stout ventromedial bristle (Fig. 12), male bacilliform sclerite densely spinose (Fig. 12). Female sternite 10 with dense patch of posteromedial setulae (Fig. 13) *A. rabida* n. sp.

Aphaniosoma arenicolum Wheeler, NEW SPECIES (Figs. 1–6)

Description.—Total length 1.2–1.4 mm. Head pale yellow, occiput and ocellar tubercle gray. Frons with inner and outer vertical bristles black, all other setae on frons and vertex reduced to small yellow setulae, interfrontal setulae slightly reclinate, uniformly distributed over frons, fronto-orbital row not distinguished from interfrontal setulae. Eye oval, long axis inclined anteroventrally. Gena broad, curved ventromedially to margins of small oral cavity; gena uniformly covered with short yellow setulae, vibrissal angle with 3–4 yellow bristles, subequal in length; vibrissal angles rounded, deflected anteromedially, almost meeting near ventral margin of face. Lunule with narrow, ventral point extended ventrally between antennae and meeting narrow median carina of face, median carina extended ventrally to below antennae, lower margin of face concave, sunken between vibrissal angles. Antennae recessed in deep foveae delimited by lunule, facial carina and vibrissal angles, pedicel and first flagellomere often not visible in lateral view; antenna



Figs. 1-6. *Aphaniosoma arenicolum*. 1, posterior segments of male abdomen, ventral. 2, male terminalia, lateral. 3, male terminalia, posterior. 4, male terminalia, anterior. 5, female terminalia, ventral. 6, female spermathecae. Scale bars = 0.05 mm (except Fig. 1 = 0.1 mm). Abbreviations: bac scl—bacilliform sclerite; cerc—cercus; epand—epandrium; hypd—hypandrium; ph—phallus; phapod—phallopodeme; sen s—sensory setulae; spr—spiracle; st—sternite; sur—surstylus; tg—tergite.

mostly yellow, apical two-thirds of arista brown or black, almost bare.

Scutum dull gray pruinose, postpronotum, notopleuron, lateral, posterolateral, and posteromedial margins of scutum yellow; scutal chaetotaxy: 1 long and 1 short postpronotal, 2 notopleurals, 1 presutural intra-alar, 1 postalar, 1 postsutural dorso-central, presutural acrostichal setulae in 8–10 rows, pale yellow. Scutellum yellow or pale brown, with 2 pairs of marginal bristles. Thoracic pleurites pale yellow, ventral half of katapisternum and meron pale brown; anepisternum posteriorly with 3–5 pale setulae and 1 longer, pale bristle; katapisternum with 2–3 pale dorsal bristles; proepisternal bristle absent.

Legs pale yellow; mid-tibia with short, dark apicoventral bristle, otherwise legs with only short yellow setulae.

Wing clear; costal margin with evenly spaced, stout, spinules from humeral vein to near apex of wing, spinules longer than diameter of costal vein; anal region and alula well-developed. Halter pale yellow.

Abdominal tergites 1–5 in male brown with yellow margins, male tergite 6 either uniformly brown or yellow with 2 lateral brown spots, abdominal tergites 1–6 in female brown with yellow margins, female tergite 7 yellow with 2 lateral brown spots. Abdominal sternites narrow, pale yellow.

Male postabdomen.—Tergite 5 and sternite 5 large, symmetrical, fifth spiracles located at ventrolateral margin of tergite 5. Tergite 6 large, symmetrical, with dense, short, lateral bristles, sixth and seventh spiracles present on both sides near ventrolateral margin of tergite 6 (Fig. 1); sternite 6 absent, position of sternite marked by pair of sensory setulae posterior to sternite 5 (Fig. 1). Tergites and sternites of segments 7 and 8 absent. Epandrium pale, narrow, sparsely setose, with posteriorly directed posteroventral projections (Fig. 2). Surstyli fused with epandrium, posteroventrally directed, narrow, longer than epandrium, densely setose on posterior and medial surfaces (Figs.

2, 3). Cerci bare, membranous, confluent medially. Bacilliform sclerites dark, densely setulose medially, expanded and rounded at point of articulation with phallic complex, narrowed distally, lateral region of bacilliform sclerite hyaline, setulose (Fig. 4). Hypandrium U-shaped in ventral view, fused with epandrium. Pregonites and gonostyli absent or fused with hypandrium. Phallapodeme long, rod-shaped; phallic guide articulated to phallapodeme and hypandrium near junction of phallapodeme with phallus. Phallus fused with phallapodeme, rigid and sclerotized, projected posteroventrally between surstyli (Fig. 2). Ejaculatory apodeme not observed, minute or unpigmented.

Female postabdomen.—Postabdomen short. Tergite 6 evenly sclerotized, sternite 6 membranous, location marked only by small bristles. Tergite 7 desclerotized medially, bristles restricted to lateral regions, sternite 7 membranous, location marked only by small bristles (Fig. 5). Tergite 8 membranous or absent, sternite 8 divided into two rounded, lateral plates, each with small bristles and setulae (Fig. 5). Tergite 10 membranous or absent, sternite 10 membranous, spinulose, broadly rounded (Fig. 5). Cerci small, with short bristles and setulae (Fig. 5). Two sclerotized, cup-shaped spermathecae present, spermathecal ducts long and coiled (Fig. 6).

Holotype ♂.—ECUADOR: Galápagos Islands: Isla Isabela: Puerto Villamil, 6.iii.1989, B. J. Sinclair, littoral zone, sweeping beach morning glories (CNC).

Paratypes.—Same data as holotype (22♂, 17♀, CNC); Isla Isabela: Puerto Villamil, 7.iii.1989, B. J. Sinclair, littoral zone, sweeping sand beach (1♂, 4♀, CNC); Puerto Villamil, 5.iii.1989, B. J. Sinclair, flamingo lagoon (2♂, 7♀, CNC); 1 km W Villamil, 1 m, 2–15.iii.1989, Peck and Sinclair, flight intercept trap (FIT), littoral scrub on sand (1♂, 3♀, CNC); Isla Santa Fé: 5.iv.1989, B. J. Sinclair, sweeping vegetation and rocks surrounding seal beach (1♂, 1♀, CNC); Isla

Española: Bahía Gardner, Om. 27.iv.1991, J. M. Heraty, beach zone (1♂, CNC); Isla Rábida: beach at NE side, Om. 10.vi.1991, J. M. Heraty (1♀, CNC); Isla Santa Cruz: Academy Bay, Charles Darwin Research Station, 25.i.1964, D. Q. Cavagnaro and R. O. Schuster, sweeping coastal plants (1♀, CAS).

Other material examined.—Isla Española, Bahía Manzanilla, 5–10.vi.1985, S. and J. Peck, littoral *Cryptocarpus* and *Prosopis*, FIT, Malaise (1♀, damaged, CNC alcohol collection).

Etymology.—The specific name is derived from the Latin *arena* (sand) and *-cola* (inhabitant), referring to the habitat of this species.

Biology.—*Aphaniosoma arenicolum* is apparently restricted to arid, saline habitats in the littoral zone. Many of the paratypes were swept from beach morning glories (*Ipomoea pes-caprae*, Convolvulaceae). Other paratypes were taken on vegetation and rocks on beaches, and at the margin of a saline lagoon inhabited by flamingos.

Remarks.—*Aphaniosoma arenicolum* is externally similar to the southern Nearctic species *A. aldrichi* Wheeler. Both species lack distinct fronto-orbital bristles, have reclinate interfrontal setulae, and have deep, sharply defined antennal foveae; these character states may be synapomorphic for this group of species. The two species may be distinguished by the color pattern of the scutum. In *A. arenicolum* the gray area on the scutum is continuous, whereas in *A. aldrichi* the scutum has four separate gray stripes.

Aphaniosoma galamarillum Wheeler,

NEW SPECIES

(Figs. 7–10)

Description.—Total length 1.1–1.4 mm. Head pale yellow. All setae on frons and vertex yellow, inner and outer vertical, outer occipital, and ocellar bristles well-developed, postocellar bristles short, convergent, 3 pairs of reclinate fronto-orbital bristles, longer posteriorly, interfrontal setulae proc-

linated, uniformly distributed over frons. Eye oval, long axis inclined anteroventrally. Gena broad, curved ventromedially to margins of small oral cavity; gena uniformly covered with short yellow setulae, vibrissal angles rounded, with 3 yellow bristles, the middle one shorter. Lunule with small ventral point extended ventrally between antennae; face concave, membranous, with very small median carina. Antennae recessed in depression delimited by lunule, orbital margins and vibrissal angles, but pedicel and first flagellomere clearly visible in lateral view; antenna mostly yellow, apical two-thirds of arista black, bare.

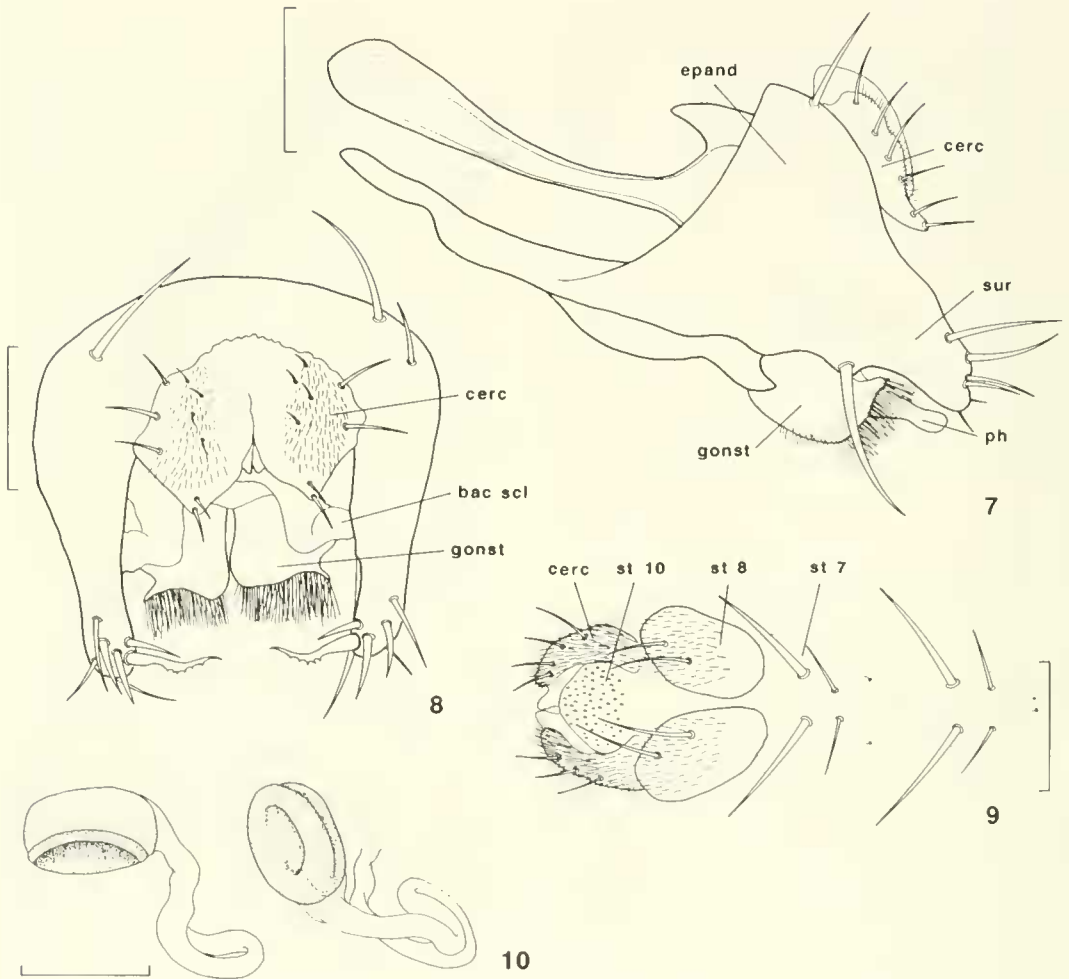
Thorax entirely pale yellow. Scutal chaetotaxy: 1 long and 1 short postpronotal, 2 notopleurals, 1 presutural intra-alar, 1 postalar, 1 intra-postalar, 2 postsutural dorso-centrals, the anterior one much shorter, 1 prescutellar acrostichal bristle, presutural acrostichal setulae in 8 rows, pale yellow. Scutellum with 2 pairs of marginal bristles. Anepisternum posteriorly with 3–5 pale setulae and 1 long bristle; katepisternum with scattered setulae and 1 long bristle; proepisternal bristle absent.

Legs pale yellow with short yellow setulae. Male hind tibia with 3 rows of longer, closely spaced setulae, 1 anterodorsal, 1 dorsal, 1 posterodorsal, setulae of anterodorsal row longer than those of other two rows, those of dorsal row weaker and more widely spaced; male hind basitarsus broad and flattened dorsoventrally, approximately twice as wide as second tarsomere and as long as remaining tarsal segments combined, basitarsus densely setulose dorsally, bare ventrally; female hindleg unmodified.

Wing clear; costal margin with weak spinules from humeral vein to near apex of wing, spinules shorter than diameter of costal vein at junction with R_1 ; anal region and alula well-developed. Halter pale yellow.

Abdominal tergites pale yellow, setose. Abdominal sternites narrow, pale yellow.

Male postabdomen.—Tergite 5 and sternite 5 large, symmetrical, fifth spiracles lo-



Figs. 7-10. *Aphanosoma galamarillum*. 7, male terminalia, lateral. 8, male terminalia, posterior. 9, female terminalia, ventral. 10, female spermathecae. Scale bars = 0.05 mm. Abbreviations: bac scl—bacilliform sclerite; cerc—cercus; epand—epandrium; gonst—gonostylus; ph—phallus; st—sternite; sur—surstylus.

cated at ventrolateral margin of tergite 5. Tergite 6 large, symmetrical, with dense, short, lateral bristles, sixth and seventh spiracles present on both sides near ventrolateral margin of tergite 6; sternite 6 absent, position of sternite marked by pair of sensory setulae posterior to sternite 5. Tergites and sternites of segments 7 and 8 absent. Epandrium pale, narrow, bare or setulose except for 3-4 long dorsal bristles (Fig. 7). Surstyli fused with epandrium; surstyli posteroventrally directed, shorter than epan-

drium, with long, strong, anterior bristle, 5-6 shorter posterior bristles and 1 pectinate ventromedial bristle (Figs. 7, 8). Cerci with bristles and setulae, pointed ventrally, confluent medially (Fig. 8). Bacilliform sclerites bare (Fig. 8). Hypandrium U-shaped in ventral view, fused with epandrium. Pregonites absent or fused with hypandrium. Gonostyli large, quadrate, densely setulose posteroventrally (Fig. 8). Phallapodeme long, rod-shaped, expanded and fan-shaped at base (Fig. 7); phallic guide absent. Phallus fused

with phallapodeme, rigid and sclerotized, projected posteroventrally between gonostyli (Fig. 7). Ejaculatory apodeme not observed, minute or unpigmented.

Female postabdomen.—Postabdomen short. Tergites 6 and 7 evenly sclerotized, bristles uniformly distributed over surface, sternites 6 and 7 pale, narrow, each with 2 short anterior, 2 long posterior bristles (Fig. 9). Tergite 8 membranous or absent, sternite 8 divided into two rounded, lateral plates, each with small bristles and setulae (Fig. 9). Tergite 10 membranous or absent, sternite 10 membranous, spinulose, broadly rounded (Fig. 9). Cerci small, with small bristles and setulae laterally (Fig. 9). Two sclerotized, cup-shaped spermathecae present, spermathecal ducts long and coiled (Fig. 10).

Holotype ♂.—ECUADOR: Galápagos Islands: Isla Isabela: iii.1989, B. J. Sinclair (CNC).

Paratypes.—Isla Isabela: 1 km W Villamil, 1 m, 2–15.iii.1989, Peck and Sinclair, flight intercept trap (FIT), littoral scrub on sand (2♀, CNC); Puerto Villamil, 6.iii.1989, B. J. Sinclair, sweeping beach morning glories in littoral zone (1♀, CNC).

Other material examined.—Isla Santa Cruz: Academy Bay, Charles Darwin Research Station, 10.v–3.vi.1985, S. and J. Peck, 30 m, arid zone, thornscrub malaise-FIT trap (1♀, damaged, CNC alcohol collection).

Etymology.—The specific name is a combination of *gal-* (from Galápagos) and *amarillum*, from the Spanish *amarilla* (yellow), referring to the type locality and the color of this species.

Biology.—Like the previous species, *Aphaniosoma galamarillum* is primarily restricted to arid, saline habitats in the littoral zone, with one specimen taken in the adjoining arid zone at an elevation of 30 m. One of the paratypes was swept from beach morning glories with many of the paratypes of *A. arenicolum*.

Remarks.—*Aphaniosoma galamarillum*

is indistinguishable from the Hawaiian species *A. minutum* Hardy (see Hardy and Delgado 1980) except on the basis of postabdominal characters. Both species have a similarly modified male hind tibia and basitarsus, suggesting that the two are sister species. Males of *A. galamarillum* may be distinguished from those of *A. minutum* by the short, relatively broad surstyli and the pectinate medial surstylar bristle.

Aphaniosoma rabida Wheeler,

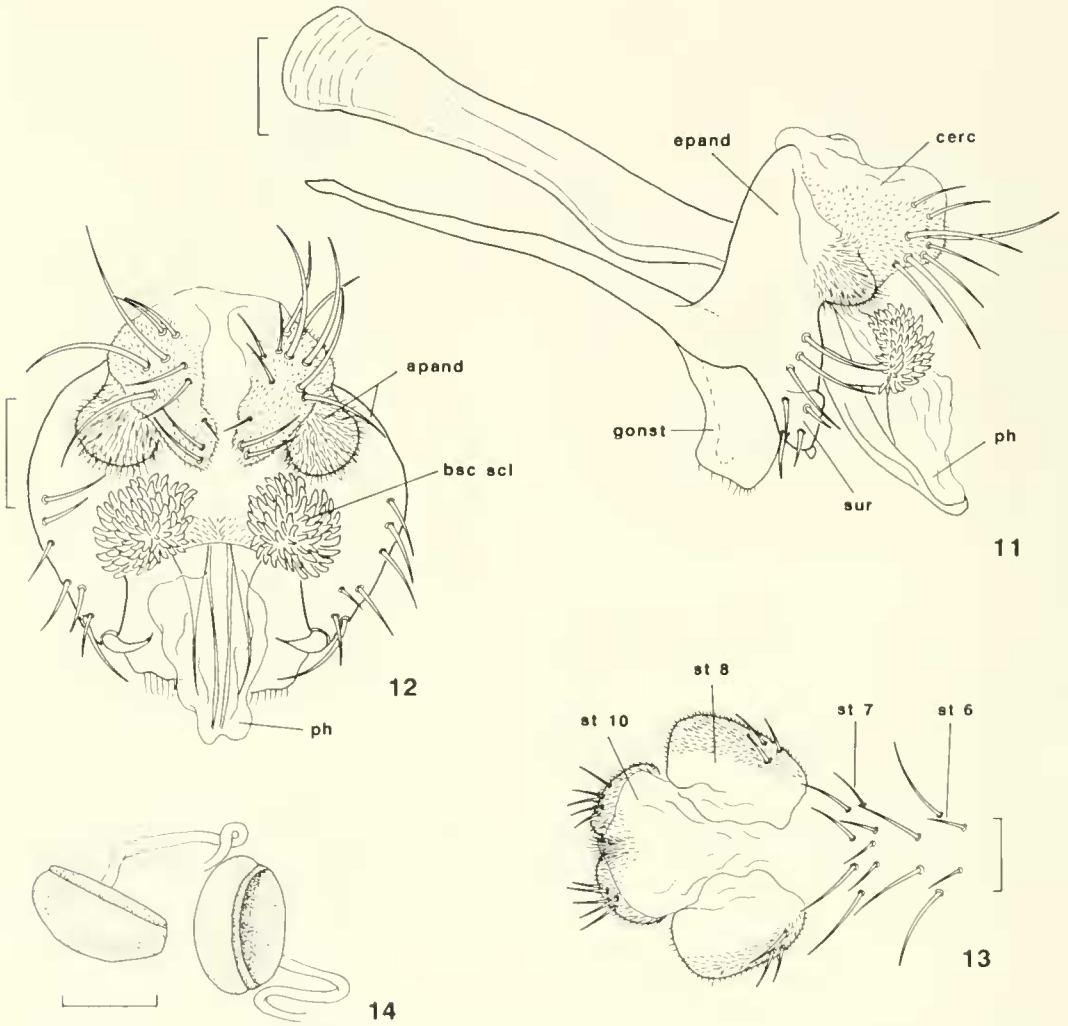
NEW SPECIES

(Figs. 11–14)

Description.—Total length 1.4–1.9 mm. Head pale yellow. All setae on frons and vertex yellow, inner and outer vertical and ocellar bristles well-developed, postocellar bristles short, divergent, 2 pairs of reclinate fronto-orbital bristles, interfrontal setulae proclinate, uniformly distributed over frons. Eye oval, long axis inclined anteroventrally. Gena broad, curved ventromedially to margins of small oral cavity; gena uniformly covered with short yellow setulae, vibrissal angles rounded, with 3 yellow bristles subequal in length. Lunule with small ventral point extended ventrally between antennae; face concave, membranous, with very small median carina. Antennae recessed in depression delimited by lunule, orbital margins and vibrissal angles, but pedicel and first flagellomere clearly visible in lateral view; antenna mostly yellow, apical two-thirds of arista black, bare.

Thorax entirely pale yellow. Scutal chaetotaxy: 1 long and 1 short postpronotal, 2 notopleurals, 1 presutural intra-alar, 2 postalar, 1 intra-postalar, 2 postsutural dorso-centrals, the anterior one much shorter, 1 prescutellar acrostichal bristle, presutural acrostichal setulae in 8 rows, pale yellow. Scutellum with 2 pairs of marginal bristles. Anepisternum posteriorly with 3–5 pale setulae and 1 long bristle; katepisternum with scattered setulae and 1 long bristle; proepisternal bristle absent.

Legs pale yellow with short yellow setu-



Figs. 11-14. *Aphanosoma rabida*. 11, male terminalia, lateral. 12, male terminalia, posterior. 13, female terminalia, ventral. 14, female spermathecae. Scale bars = 0.05 mm. Abbreviations: bac scl—bacilliform sclerite; cerc—cercus; epand—epandrium; gonst—gonostylus; ph—phallus; st—sternite; sur—surstylus.

lae: mid-tibia with strong, yellow apicoven-
tral bristle.

Wing clear: costal margin with weak spin-
ules from humeral vein to near apex of
wing, spinules shorter than diameter of cos-
tal vein at junction with R_1 ; anal region and
alula well-developed. Halter pale yellow.

Abdominal tergites pale yellow, setose,
occasionally with pale brown anterior spots.
Abdominal sternites narrow, pale yellow.

Male postabdomen.—Tergite 5 and ster-

nite 5 large, symmetrical, fifth spiracles lo-
cated at ventrolateral margin of tergite 5.
Tergite 6 large, symmetrical, with dense,
short, lateral bristles, sixth and seventh spi-
racles present on both sides near ventrolat-
eral margin of tergite 6; sternite 6 absent,
position of sternite marked by pair of sen-
sory setulae posterior to sternite 5. Tergites
and sternites of segments 7 and 8 absent.
Epandrium pale, narrow, with setulose pos-
teromedial lobe and 3 long bristles dorsal

to surstylus (Figs. 11, 12). Surstyli partially fused with epandrium, ventrally directed, shorter than epandrium, with 4 long lateral bristles and 1 short, stout ventromedial bristle (Figs. 11, 12). Cerci membranous, setulose, with several long bristles (Figs. 11, 12). Bacilliform sclerites expanded posteriorly into a pair of dark, rounded, densely spinose lobes (Fig. 12). Hypandrium U-shaped in ventral view, fused with epandrium. Pregonites absent or fused with hypandrium. Gonostyli large, quadrate, sparsely setulose ventrally (Fig. 11). Phallopodeme long, rod-shaped (Fig. 11); phallic guide absent. Phallus fused with phallopodeme, rigid and sclerotized, with membranous dorsal region, projected posteroventrally (Fig. 11). Ejaculatory apodeme not observed, minute or unpigmented.

Female postabdomen.—Postabdomen short. Tergites 6 and 7 evenly sclerotized, bristles uniformly distributed over surface, sternites 6 and 7 membranous, location marked only by small bristles (Fig. 13). Tergite 8 membranous or absent, sternite 8 divided into two rounded, lateral plates, each with small bristles and setulae (Fig. 13). Tergite 10 membranous or absent, sternite 10 membranous, posteriorly setulose, broadly rounded (Fig. 13). Cerci small, with small bristles and setulae laterally (Fig. 13). Two sclerotized, cup-shaped spermathecae present, spermathecal ducts long and coiled (Fig. 14).

Holotype δ .—ECUADOR: Galápagos Islands: Isla Rábida: beach on NE side, 10.vi.1991, J. M. Heraty (CNC).

Paratypes.—Same data as holotype (8 δ , 7 η , CNC).

Etymology.—The specific name is a noun in apposition referring to the type locality of this species.

Biology.—There is no detailed biological information associated with the type specimens. Like the other species of *Aphaniosoma* from the Galápagos, they were taken in the littoral zone just above sea level.

Remarks.—There are no clear synapo-

morphies linking *A. rabida* to any other described species. It superficially resembles the Hawaiian species *A. macalpinei* Hardy, but the male postabdomen is distinctly different. The placement and affinities of *A. rabida* remain unknown pending a complete revision of *Aphaniosoma*.

DISCUSSION

Male postabdominal structure in Aphaniosoma: Griffiths (1972) provided the first detailed treatment of the male postabdomen of the Chyromyidae, although his analysis was based on examination of only two species, *Chyromya flava* (L.) and *Aphaniosoma occulicauda* Collin, and only *C. flava* was illustrated. McAlpine (1987) also discussed the male postabdomen of the Chyromyidae but again only *C. flava* was illustrated. Because both authors based their analyses on very few species they underestimated the structural diversity in the family and misinterpreted certain structures, especially in *Aphaniosoma*. Many of the characters used by Griffiths (1972) and McAlpine (1987) in their diagnoses of the family are characters which, although apparently present in the groundplan of the Chyromyidae, are lost in some or all lineages of *Aphaniosoma*. These characters include an expanded distiphallus with complex sclerotization (Griffiths 1972, McAlpine 1987), a phallus capable of being swung through a wide arc to an anteriorly directed rest position (Griffiths 1972), and an extensive connection between the phallopodeme and hypandrium via a well-developed phallic guide (Griffiths 1972, McAlpine 1987) (Griffiths attributed the well-developed phallic guide to the groundplan of Chyromyidae and did not comment on its distribution within the family).

Griffiths (1972) did not establish the position of the abdominal spiracles in *Aphaniosoma* due to the small size of the specimens. Specimens cleared in lactic acid in this study confirm that the distribution of spiracles in *Aphaniosoma* is the same as in

Chyromya. The sixth and seventh pairs are present on both sides and located near the ventrolateral margin of tergite 6.

Although Griffiths (1972) stated that tergite 6 in *Aphaniosoma* is divided into two lateral pieces, the tergite is undivided in the species examined in this study. Sternite 6, tergite and sternite 7 and tergite 8 are absent. Sternite 8 is membranous in the species examined in this study. Griffiths (1972) interpreted all these sclerites as absent in *Aphaniosoma*; McAlpine (1987) stated that syntergosternite 7+8 is fused dorsally with the epandrium but did not indicate exactly which components he believed to comprise the syntergosternite.

Griffiths (1972) considered the lateral fragments of tergite 6 the last dorsal sclerites of the abdomen in *Aphaniosoma*, with the epandrium (his 'periandrium') and cerci reduced and membranous. Although the distribution of this state should be confirmed throughout the genus, it does not apply to the species examined in this study. Evidence refuting Griffiths' statement includes the articulation of the hypandrium and surstyli with the last dorsal sclerite and the location of the bacilliform sclerites beneath it. All of these landmarks identify the last dorsal abdominal sclerite as the true epandrium. Also, the cerci are clearly evident posterior to the epandrium and flanking the anus.

The status of the gonostyli and pregonites is problematic and requires clarification throughout the genus. Both Griffiths (1972) and McAlpine (1987) characterized the Chyromyidae as having well-developed gonostyli (postgonites, parameres). McAlpine described the pregonites (his 'gonopods') as present with strong bristles; Griffiths did not mention pregonites. There is a pair of large, broad, sclerotized gonostyli in *A. galamarillum* and *A. rabida*, articulated to the posteromedial region of the hypandrium, projected ventrally, and flanking the phallus. The articulation point and position

confirm the identity of these structures. The pregonites in these species are absent or fused with the hypandrium or gonostyli.

Both the pregonites and gonostyli are fused with the hypandrium or absent in *A. arenicolum*. There is a pair of dark, sclerotized structures that articulate anterodorsally with the junction of the phallus and phallopodeme, and project posteroventrally alongside the distiphallus to an articulation with the inner wall of the surstyli (Fig. 4, bac scl). These structures are densely setulose ventromedially. They continue laterally as a hyaline, setulose region that also originates near the base of the phallus and projects posteroventrally toward the inner wall of the surstyli. The hyaline region appears to be connected to a second pair of narrow hyaline arms that project posteriorly toward the cerci. Based on the articulation points of these structures we conclude that the entire structure is the bacilliform sclerite. Although the structures bear a superficial resemblance to the gonostyli in other Chyromyidae, the articulation of this structure with the base of the phallus and the inner wall of the surstyli provides strong support for our interpretation. Gonostyli, in contrast, articulate with the hypandrium, usually via the pregonites, near the point of articulation between the hypandrium and the phallic complex, and project ventrally or posteroventrally lateral to the distiphallus. Our interpretation, although supported by the morphological evidence at hand, should be considered provisional until a broader analysis of postabdominal structure in the Chyromyidae is undertaken.

Relationships and origin of the Galápagos Chyromyidae: Most insect species recorded from the Galápagos Islands appear to be derived from colonizing ancestors that originated in Mexico, Central America and western South America (Peck 1991). The paths of ocean currents and prevailing winds are suitable for carrying organisms from the Americas to the islands for much of the year

(Peck and Kukalová-Peck 1990). The western Pacific is the source for a very small component of the fauna (Peck 1991).

Peck and Kukalová-Peck (1990) analyzed the Coleoptera fauna of the archipelago and concluded that the present Galápagos beetle fauna (335 species) arrived in the islands by at least 257 separate colonization events. Of the 313 species of beetles not introduced by humans, 60%, primarily those in the littoral, arid, and transition zones, arrived via rafting on vegetation or other flotsam. Most of the rest of the fauna (39%) arrived by active flight or as aerial plankton carried by prevailing winds (Peck and Kukalová-Peck 1990).

Diptera species adapted to life in the littoral zone would be expected to have a high salt tolerance and to survive periodic inundation by seawater. As such, these species could be expected to have a higher survival capability in rafting events than species adapted to more inland habitats. In addition, the tendency of littoral Diptera to aggregate on vegetation may make them more susceptible to being transported on rafts of vegetation. Preliminary analysis of the Galápagos Diptera fauna indicates a high species diversity in the littoral zone. At least 32 species of flies are restricted to the littoral zone, significantly more than are restricted to other inland zones (Sinclair, unpublished data). This species diversity may be due in part to higher survival of halophilic Diptera in transit to the islands.

The extremely small size of individuals of *Aphaniosoma* makes them good candidates for long-distance dispersal in aerial plankton. The occurrence of *Aphaniosoma* on many isolated oceanic islands may be the result of a preadaptation to both rafting and aerial dispersal.

The presence of two chyromyid species with apparent sister species in other regions and a third species (*A. rabida*) apparently unrelated to the other two, suggests three separate colonizations of the Galápagos.

There is morphological evidence that *Aphaniosoma arenicolum* belongs to a monophyletic group which also includes *A. aldrichi* from Texas and two undescribed species from southern California. Putative synapomorphic characters supporting this clade include the dense reclinate interfrontal setulae, the loss of fronto-orbital bristles, and deep, well-defined, antennal foveae. It appears, therefore, that the affinities of *A. arenicolum* lie in the southern Nearctic Region.

One of the few groups of Galápagos Diptera for which phylogenetic relationships are well resolved is the family Ceratopogonidae. Five of the six widespread species of Ceratopogonidae on the Galápagos also occur in the Nearctic Region and two of the species are known only from the Nearctic and Galápagos (Borkent 1991). Borkent (1991) suggested that these disjunctions may be the result of inadequate sampling in Central and South America. If the two ceratopogonid species do occur in those regions, then it is likely that the species on the Galápagos dispersed to the islands naturally via rafting or as aerial plankton. If the disjunction proves to be a real one, it is likely that the species were carried from the Nearctic to the Galápagos by human activity (Borkent 1991). Four species of Ceratopogonidae endemic to the Galápagos have putative sister species on the Neotropical mainland. This implies four separate colonization events from the Americas followed by allopatric speciation on the Galápagos (Borkent 1991).

Aphaniosoma galamarillum is the apparent sister species to the Hawaiian species *A. minutum*, based on the modified male hindleg. The sister group to this species pair is unknown. While a Neotropical origin would be most likely for *A. galamarillum*, based on evidence from other Galápagos insects, this is not the case for *A. minutum*. Most of the Hawaiian insect fauna has Asian affinities; only 5% of the Hawaiian insects ap-

pear to be derived from an American source (Peck and Kukalová-Peck 1990). Until the sister group of these two species is known nothing can be concluded about the source area or movements of the group.

It is difficult to speculate on the overall distribution patterns of *Aphaniosoma* beyond the discussion above because many species remain undescribed, and because there is no hypothesis on the relationships between the species, or even on the monophyly of the genus. Because most Galápagos insects whose affinities and source areas are known originated on the Pacific coast of Central and South America, it is probable that the Galápagos *Aphaniosoma* also originated there. Although members of the family Chyromyidae are rarely collected in large numbers, efforts to collect in arid littoral zone areas on the Pacific coast may yield additional specimens of *Aphaniosoma* which are conspecific or closely related to the Galápagos fauna.

ACKNOWLEDGMENTS

Field work in the Galápagos was permitted by the Galápagos National Park Service, Department of Forestry, Ministry of Agriculture, Ecuador and logistic support was furnished by the Charles Darwin Research Station, Isla Santa Cruz. Funding for field work in the Galápagos was provided by a Natural Sciences and Engineering Research Council of Canada grant to S. B. Peck (Carleton University). We thank P. H. Arnaud, Jr. (CAS) and A. L. Norrbom (USNM) for loans of specimens. Laboratory facilities for the authors were provided by the Biological Resources Division, CLBRR, Agriculture Canada. J. M. Heraty and J. E. O'Hara (Agriculture Canada, Ottawa) and S. B. Peck commented on the manuscript.

LITERATURE CITED

- Becker, T. 1903. Aegyptische Dipteren (Fortsetzung und Schluss). Mitteilungen aus dem Zoologischen Museum in Berlin 2(3): 67-195.
- Borkent, A. 1991. The Ceratopogonidae (Diptera) of the Galápagos Islands, Ecuador with a discussion of their phylogenetic relationships and zoogeographic origins. *Entomologica Scandinavica* 22: 97-122.
- Cogan, B. H. 1980. Family Chyromyidae, pp. 628-629. In Crosskey, R. W., ed., *Catalogue of the Diptera of the Afrotropical Region*. British Museum (Natural History), London. 1437 pp.
- Cumming, J. M. and B. J. Sinclair. 1990. Fusion and confusion: interpretation of male genitalia homologies in the Empidoidea (Diptera). Abstract Volume, Second International Congress of Dipterology, Bratislava, Czechoslovakia, August 27-September 1, 1990. p. 334.
- Ebejer, M. J. 1993. The Chyromyidae of Malta, with descriptions of new species of *Aphaniosoma* (Dipt., Schizophora). *Entomologist's Monthly Magazine* 129: 125-133.
- Griffiths, G. C. D. 1972. The phylogenetic classification of Diptera Cyclorrhapha with special reference to the structure of the male postabdomen. Dr. W. Junk, The Hague. Series Entomologica 8: 1-340.
- . 1981. Book Review, *Manual of Nearctic Diptera*, Volume 1. *Bulletin of the Entomological Society of Canada* 13: 49-55.
- Hardy, D. E. and M. D. Delfinado. 1980. *Insects of Hawaii*. Volume 13. Diptera: Cyclorrhapha III. University of Hawaii Press, Honolulu. 451 pp.
- McAlpine, J. F. 1981. Morphology and Terminology—Adults, pp. 9-63. In McAlpine, J. F., et al., coords., *Manual of Nearctic Diptera*, Volume 1. Research Branch Agriculture Canada Monograph 27: 1-674.
- . 1987. Family Chyromyidae, pp. 985-988. In McAlpine, J. F., ed., *Manual of Nearctic Diptera*, Volume 2. Research Branch Agriculture Canada Monograph 28: 675-1332.
- Melander, A. L. 1913. A synopsis of the dipterous groups Agromyzinae, Milichiinae, Ochthiphilinae and Geomyzinae. *Journal of the New York Entomological Society* 21: 283-300.
- Peck, S. B. 1991. Evolution on Island Archipelagos. The Galápagos Archipelago, Ecuador: With an emphasis on terrestrial invertebrates, especially insects; and an outline for research, pp. 319-336. In Dudley, E. C., ed., *The Unity of Evolutionary Biology; Proceedings of the 4th International Congress of Systematics and Evolutionary Biology (ICSEB IV)*, Volume 1. Dioscorides Press, Portland, Oregon. 588 pp.
- Peck, S. B. and J. Kukalová-Peck. 1990. Origin and biogeography of the beetles (Coleoptera) of the Galápagos Archipelago, Ecuador. *Canadian Journal of Zoology* 68: 1617-1638.
- Pitkin, B. R. 1989. Family Chyromyidae, p. 600. In Evenhuis, N. L., ed., *Catalog of the Diptera of the Australasian and Oceanian Regions*. Bishop Museum Press, Honolulu. 1155 pp.

- Soós, Á. 1984. Family Chyromyidae, pp. 56–60. *In* Soós, Á. and L. Papp, eds., Catalogue of Palaearctic Diptera. Volume 10. Clusiidae—Chloropidae. Akadémiai Kiadó, Budapest. 402 pp.
- Steyskal, G. C. 1977. Family Chyromyidae, p. 240. *In* Delfinado, M. D. and D. E. Hardy, eds., Catalog of the Diptera of the Oriental Region. Volume III. Suborder Cyclorrhapha (excluding Division Aschiza). University Press of Hawaii, Honolulu. 854 pp.
- Wood, D. M. 1990. Ground plan of the male genitalia of Brachycera (Diptera), Abstract Volume, Second International Congress of Dipterology, Bratislava, Czechoslovakia, August 27–September 1, 1990, p. 363.
- Wood, D. M. 1991. Homology and phylogenetic implications of male genitalia in Diptera: The ground plan, pp. 255–272. *In* Weissmann, L., I. Országh, and A. C. Pont, eds., Proceedings of the Second International Congress of Dipterology. SPB Academic Publishing, The Hague. 367 pp.